A SEVEN YEAR STUDY OF THE LIFE CYCLE OF THE MAYFLY *EPHEMERA DANICA*

CYRIL BENNETT

[*]*Dr C.J. Bennett, The John Spedan Lewis Trust for the Advancement of the Natural Sciences, Leckford Estate, Leckford, Stockbridge, Hampshire, SO20 6JF, UK*
Email: cyril.bennett@yahoo.co.uk

Introduction

Ephemera danica Müller, 1764 (Ephemeroptera) is one of the largest mayflies found in the British Isles with some females reaching over 30 mm. It is a common and widespread species found in rivers, lakes and streams throughout Europe and is particularly abundant in many of the lowland rivers of the British Isles. The larvae are burrowers – mainly found where silt accumulates below macrophytes.

This article gives a general overview of research work on the factors affecting the life cycle of *Ephemera danica* over a seven year period (1995–2002) on two rivers, the River Test at Leckford in Hampshire and the North Wey at Tilford in Surrey. The River Test rises from springs in the chalk at Ashe, near Overton, in Hampshire and flows for almost 40 miles in a southerly direction cutting across Salisbury Plain and passing through Stockbridge and Romsey to enter the sea at Southampton Water. The North Wey rises in chalk springs just above Alton in Hampshire and flows north-east over Upper Greensand, entering Surrey near Farnham, and then flows south to its confluence with the South Wey at Tilford and then on to join the Thames at Weybridge.

The site at Leckford was a 50 metre stretch of a ‘carrier’ stream with a mean width of about 6 metres and a mean depth of 60 cm. The site at Tilford was a similar 50 metre stretch of the main river, with a mean width of about 5 metres and a mean depth of 50 cm. There were numerous weed-beds at both sites which consisted mainly of water crowfoot (*Ranunculus* spp.) and starwort (*Callitriche* spp.) and both sites were known to hold good populations of *E. danica*. Samples were taken in the gravel and in the sediments beneath the weed-beds using a 0.1 m^2 Surber sampler.

Life cycle of *E. danica*

The main emergent period of the adults is in late May and early June when, in common with all other mayflies, they pass through two winged stages,

[*] Current address: 9 East Mill Green, Bentley, Ipswich, Suffolk IP9 2BW, UK.

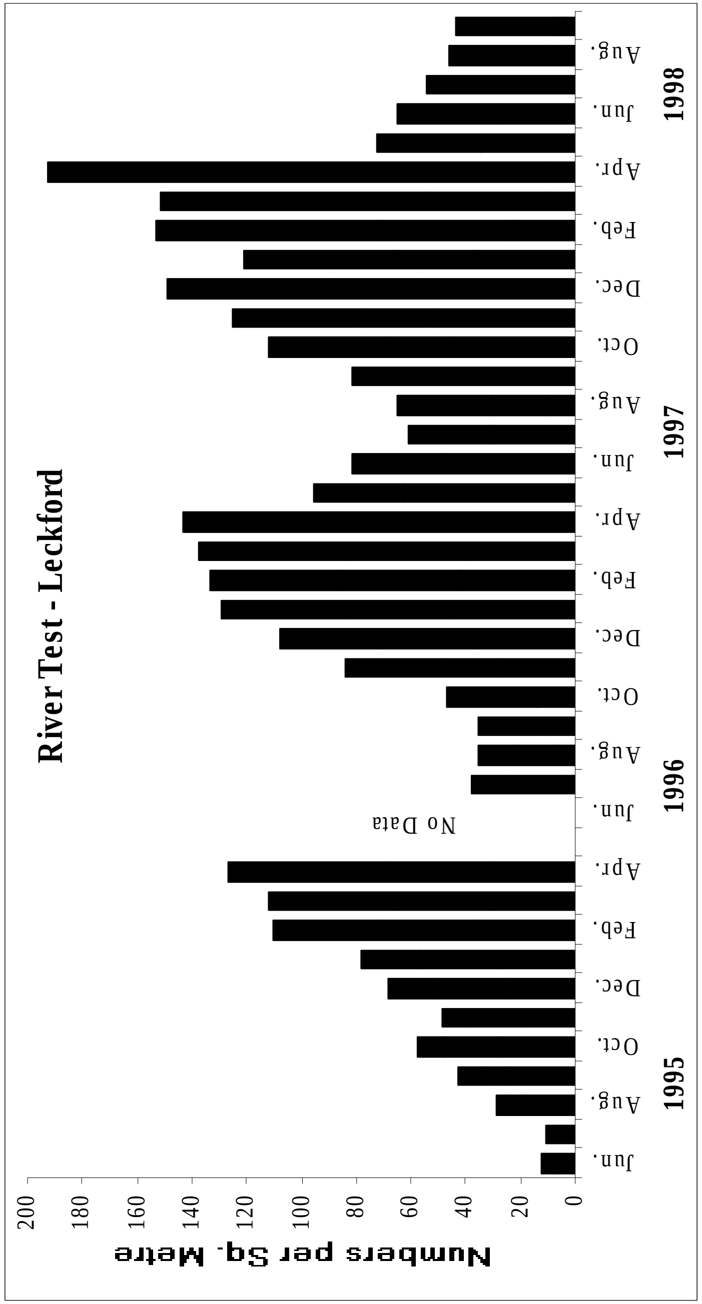


FIG. 1. Population densities of *E. danica* at Leckford over a four year period showing a steady rise in numbers each year up to the main emergent period in May.

the subimago and the imago. While there has been much debate on the length of the life cycle of *E. danica* (one, two or three years), it has generally been recorded as having a two-year life cycle (review by Elliott et al. 1988). A nine year study by Wright et al. (1981) on the River Lambourn in southern England also found a two year cycle and Tokeshi (1985) has suggested that, based on the degree/days of growth, at least the larger females cannot reach a mature size in less than two years. However, the present study shows that both males and females can reach maturity in a single year depending on water temperatures.

Population densities and adult emergence patterns

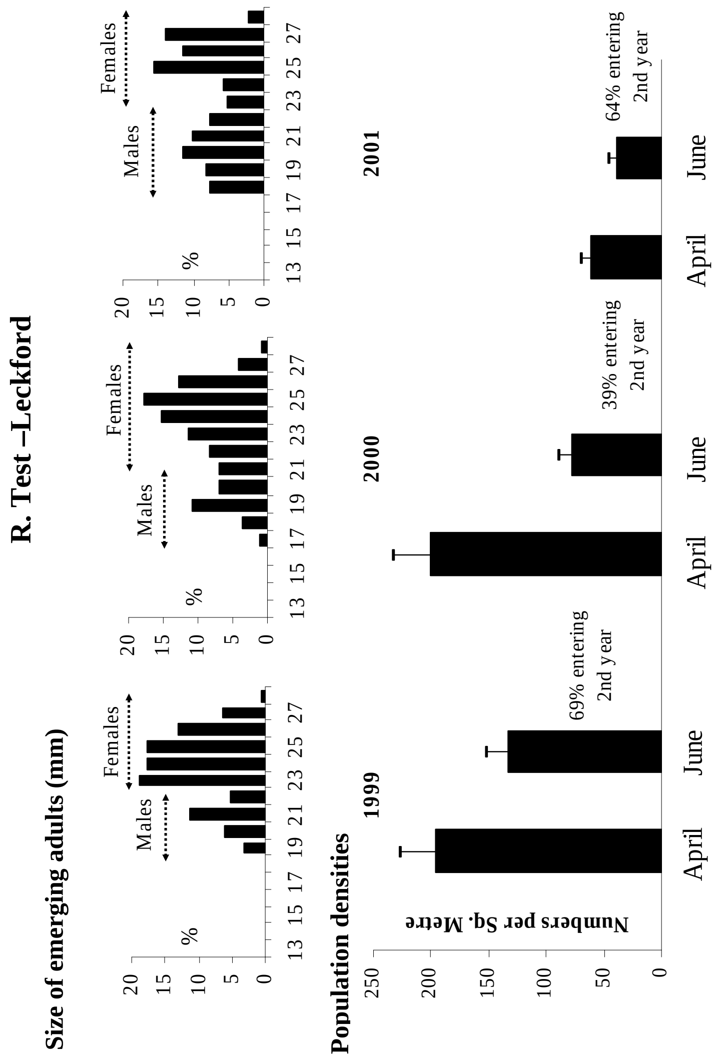
Monthly sampling at each site (Bennett 1996, 2002) showed that recruitment of newly hatched larvae increases steadily to produce a peak population density in early spring, just before the main adult emergent period; most of the larvae remaining in July and August will then enter a second year. Fig. 1 shows the population densities at Leckford over a four year period and Fig. 2 shows that while those entering a second year at Leckford can usually account for the number of adults emerging the following year, those at Tilford need to be heavily supplemented by larvae reaching maturity in a single year. Fig. 2 also shows that the sizes of adults emerging at Tilford were significantly smaller than those at Leckford, particularly females which tended to merge into the smaller size ranges of males.

In order to establish why this was happening, the developing stages of both eggs and larvae were examined at each site.

Egg development

Fig. 3a shows the number of days for *E. danica* eggs to hatch when incubated at various water temperatures. Eggs where stripped from fertilised female imagos returning to the water at both sites in late May and incubated in rainwater in the laboratory at controlled temperatures of 30 °C, 24 °C, 16 °C, 10 °C, 5 °C and at mean room temperatures of 23.8 °C and 20 °C. Eggs were also incubated in the river in tethered containers where accurate water temperatures were monitored at 30-minute intervals using permanently sited temperature logging equipment (recording to an accuracy of +/- 0.2 °C).

In common with a number of other mayfly species (Elliott 1972, Humpesch 1980, Humpesch & Elliott 1980, review by Elliott & Humpesch 1983), the relationship between the number of days needed for the eggs to hatch after fertilisation (X), and the water temperature (Y) can be described by a two parameter power function $Y=aX^{-b}$, as shown by the trend line.



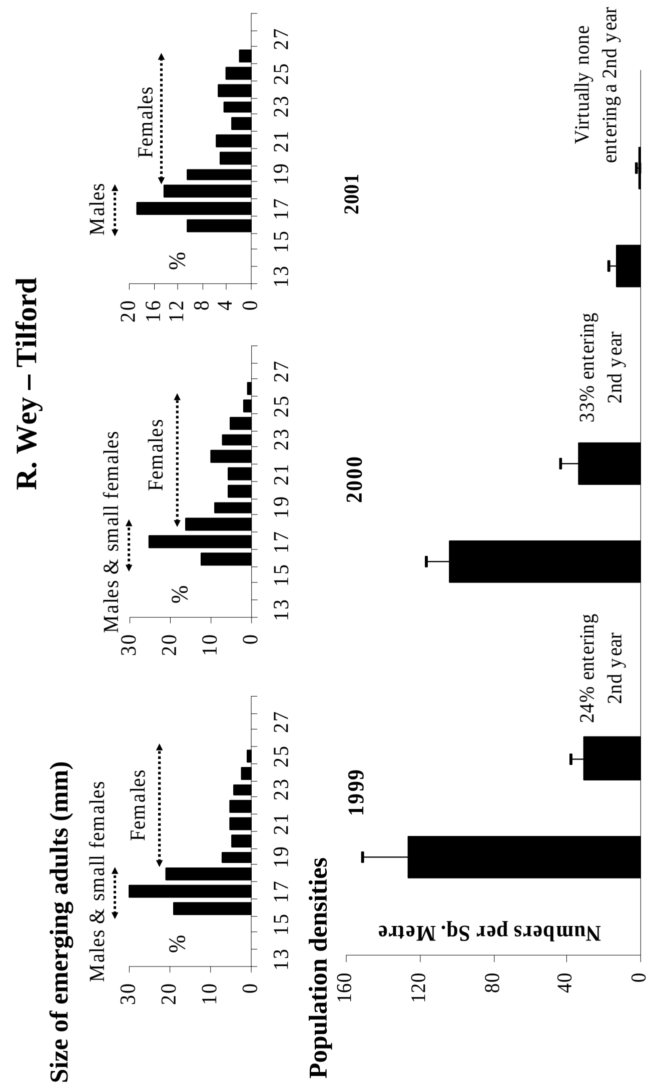


FIG. 2. *(this and facing page)* Mean population densities of *E. danica* at each site just before (April) and just after (June) the main emergent period. Graphs above each year show the size of the emerging adults. Error bars = 95 % confidence limits.

In each case, well over 50 % of the eggs hatched with the exception of those incubated at 30 °C, where about 98 % of the eggs aborted. Eggs taken from both sites and incubated in rainwater at a mean temperature of 20 °C hatched in 11 days, while those incubated at 5 °C had only reached a third of the way through development after 70 days. Those incubated in the river at Tilford (North Wey) in both river and rainwater, hatched in 24 days at a mean temperature of 14.25 °C and this was also the case with those incubated in the South Wey at a mean temperature of 13.7 °C.

Based on these data, together with accurate monitoring of water temperatures at both sites, it could be seen that the eggs at Tilford would hatch in 19 days, two days before those at Leckford. Water temperatures at Tilford remained above those at Leckford (mean difference = 0.6 ºC) during the early larval stages leading to a much earlier appearance of small first year larvae at Tilford (Fig. 3b).

Growth rates

Growth rates of larvae at each site were recorded monthly over a full year, and as field growth rates for a semivoltine species are difficult to interpret due to the overlapping nature of year classes, small first year larvae (3–5 mm) were taken from each site in September and kept in two isolation tanks containing water and sediments from the corresponding river. Each tank contained 150 larvae and was covered with muslin to facilitate the collection and measurement of any adults that emerged. Both tanks were kept in an unheated outhouse with water temperatures checked daily. The tanks were maintained (weekly) with fresh supplies of river water and sediments, and to ensure that no unwanted invertebrates were introduced, fresh sediments were thoroughly ground between the fingers before being added to the tanks. Larvae were measured (body length) at the end of each month and these were then compared with field growth rates recorded at each site (Fig. 4).

Recruitment began much earlier at Tilford with small (4–5 mm) larvae appearing by early August. This gave them a head start over those at Leckford where first year larvae of this size did not appear until late September. Rapid growth of first year larvae at both sites meant that they quickly started to overlap into the size ranges of second year larvae and by the following spring a high proportion had merged into many of the size ranges of mature second year larvae at both sites. However, none attained the larger female size ranges of those at Leckford which, after a two year growth period, could reach up to 29 mm; females emerging after a single year were therefore much smaller. Most of the larvae kept in the isolation tanks emerged as adults after a single year with sizes ranging from 13–16 mm for males and 17–21 mm for females.

a)

b)

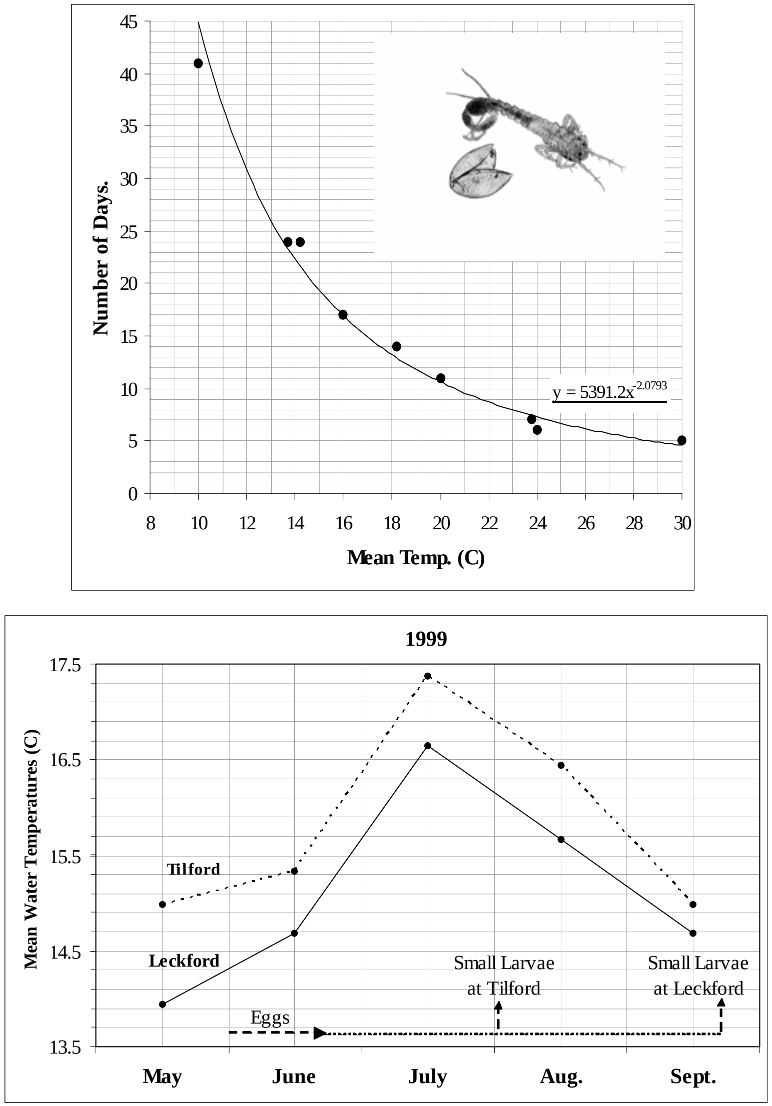


FIG. 3. (a) Number of days for *E. danica* eggs to hatch at various temperatures and (b) mean monthly water temperatures at each site during the egg and early larval stages; eggs at Tilford hatched two days before those at Leckford. Temperatures were recorded at 30-minute intervals using permanently sited equipment.

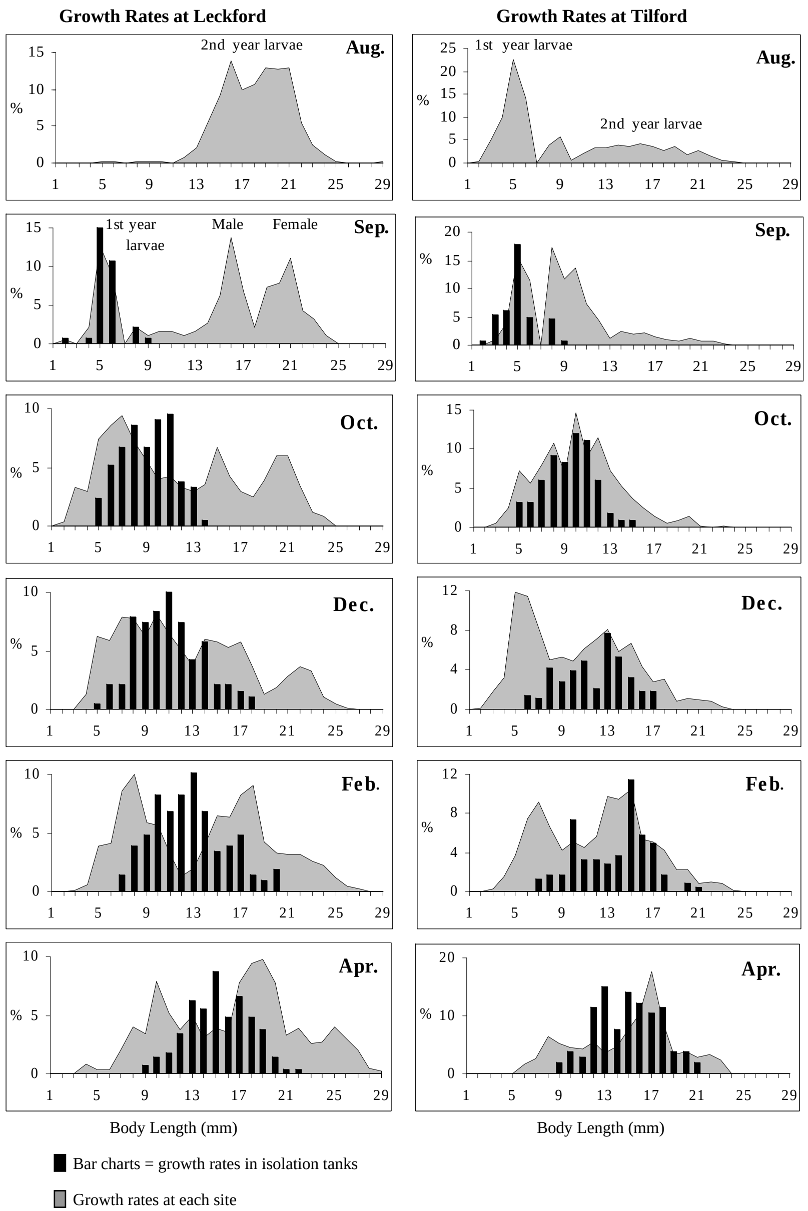


FIG. 4. Growth rates of *E. danica* larvae at each site compared with growth rates of larvae kept in each isolation tank.

There was further recruitment of small larvae at both sites throughout the winter months (Fig. 4) but the growth rates of these were much slower and would therefore need a second year of growth to reach maturity.

The mainly two-year growth period at Leckford produced a clear separation into male and female bimodal size classes early in the second year (Fig. 4) but no such separation could be seen in the relatively few larvae that entered a second year at Tilford. What appears to be a ‘male’ peak at Tilford in April was in fact a mixture of both males and small females (Figs 2 & 4).

Water temperatures

Although mean water temperatures were significantly higher at Tilford during the summer months (Fig. 3b), they fell below those at Leckford in October and remained significantly lower during the winter months. Water temperatures in the isolation tanks were initially higher than those recorded at both sites resulting in faster growth rates in the first year larvae (Fig. 4) but during the rest of the winter months the mean water temperatures in the tanks generally remained between those recorded at each site.

By increasing the mean water temperature to 20 °C in a further isolation tank, it was found that growth rates were accelerated to such an extent that larvae could reach a mean size of over 14 mm in just four months from hatching, with some even reaching 19 mm.

Analysis of gut contents

As food availability could influence growth rates at each site, it was important to compare feeding habits by analysing the gut contents of *E. danica* larvae. To limit any source of error and to ensure that random samples were recorded, a method similar to that described by Brown (1961) was used and as the fore-gut contents of *E. danica* larvae from both rivers consisted almost entirely of plant detritus, the relative amounts of food consumed at each site were compared using a colorimeter to measure the turbidity of each suspension; these were replicated to ensure accuracy. Fig. 5 clearly shows that Leckford larvae had a higher food content than those at Tilford throughout the year. The increase in feeding at both sites up to April was mainly due to the increasing size of the larvae used for gut analysis, but this increase was much greater in Leckford larvae. Although the size of the second year larvae used between May and August remained fairly constant, feeding at both sites increased during July and August.

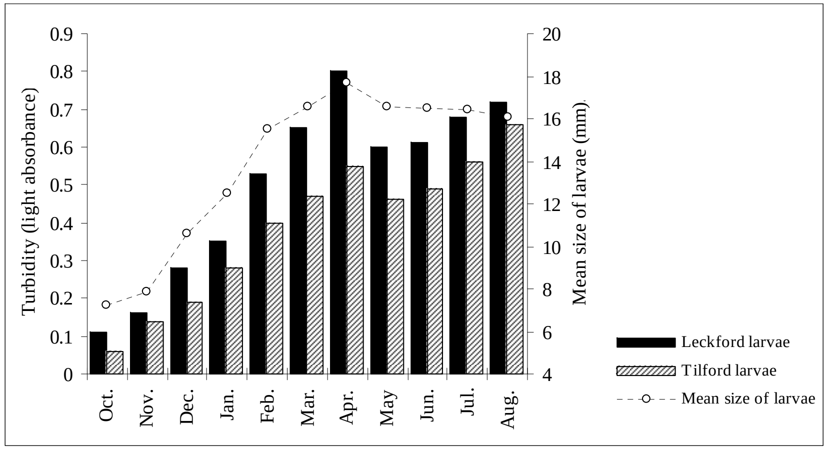


FIG. 5. Gut contents of larvae at each site showing the total food content measured as the turbidity of each suspension. The dotted line gives the mean size of the larvae used.

Conclusions

This study has questioned the widely held view that *Ephemera danica* needs two years to complete its life cycle and clearly shows that this species can complete in a single year. Although it has been suggested that at least the larger females need two years to mature (Tokeshi 1985), this study shows that both males and females can complete in a single year. However, those females that did complete in a year were significantly smaller than those taking two years which would result in the production of fewer eggs, from around 6000 in a 24 mm female down to 3000 in an 18 mm female (Bennett 1996). Although the majority of Tilford larvae completed their life cycle in a single year, the food content in the larvae was significantly less than that found in Leckford larvae.

The predominantly one-year cycle at Tilford clearly stemmed from the much earlier recruitment of small (3–5 mm) larvae, up to six weeks before those at Leckford and this appears to be quite normal at this site; they can even appear in late July (Bennett 1996). This is almost certainly due to the higher summer water temperatures at Tilford. It has also been shown that the normal two-year life cycle of the stonefly *Leuctra nigra* can be shortened to one year at high temperatures in the laboratory (Elliott 1987).

Although there are no reliable data to show the extent to which summer water temperatures may have increased, earlier work on *E. danica* (Hills 1934, Courtney Williams 1949) indicates that water temperatures were

generally lower than those recorded during this study. This would have meant that during that period, it would have been unlikely for *E. danica* to complete its life cycle in less than two years but with increasing water temperatures on many of our rivers, *Ephemera danica* populations are probably moving more towards a one-year cycle. This can have serious disadvantages because a period of bad weather during the relatively short emergent period, when most of the population would be in the adult stage, could severely reduce or even wipe out a population. This was seen at Tilford in 2000 (Fig. 2) when most of the population was lost after prolonged high winds and heavy rain prevented large numbers of females from returning to the water to lay their eggs. Samples taken in September showed that there was very little recruitment of first year larvae resulting in a very low population the following April.

Acknowledgements

I would like to thank Dr Malcolm Crabtree, Managing Director of the Leckford Estate for the use of the river site at Leckford and Mr Guy Robinson, Head River Keeper of The Leckford Estate, for his assistance during this survey.

I would also like to thank Commander Warren Gilchrist (Chairman of The John Spedan Lewis for the Advancement of the Natural Sciences) for his considerable help during this study; the Frensham Fly Fishers for the use of their site at Tilford; Dr Adeline Wong of University College Chichester for her help with the egg incubation experiments; and Prof. J.M. Elliott for comments and suggestions for improvement of the manuscript.

I must also thank my wife Marie for her help with the endless task of counting and measuring many thousands of mayfly larvae.

References

Bennett, C.J. (1996). The ecology of mayflies (Ephemeroptera) in the upper reaches of the river Wey in Surrey. PhD thesis, University of London, UK (unpublished).

Bennett, C.J. (2002). *A seven year study of the life cycle of the mayfly* Ephemera danica *(Ephemeroptera) on two rivers in southeast England*. The John Spedan Lewis Trust for the Advancement of the Natural Sciences – Record No. 7 (unpublished).

Brown, D.S. (1961). The food of the larvae of *Cloeon dipterum* L. & *Baetis rhodani* (Pictet) (Insecta, Ephemeroptera). *Journal of Animal Ecology* **30**, 55-75.

Courtney Williams, A. (1949). *A dictionary of trout flies.* Adam & Charles Black, London. 376 pp.

Elliott, J.M. (1972). Effect of temperature on the time of hatching in *Baetis rhodani* (Ephemeroptera: Baetidae). *Oecologia* **9**, 47-51.

Elliott, J.M. (1987). Temperature-induced changes in the lifecycle of *Leuctra nigra* (Plecoptera: Leuctridae) from a Lake District stream. *Freshwater Biology* **18**, 177-184.

Elliott, J.M. & Humpesch, U.H. (1983). *A key to the adults of the British Ephemeroptera with notes on their ecology*. Scientific Publication No. 47. Freshwater Biological Association, Ambleside. 97 pp.

Elliott, J.M., Humpesch, U.H. & Macan, T.T. (1988). *Larvae of the British Ephemeroptera. A key with ecological notes*. Scientific Publication No. 49. Freshwater Biological Association. Ambleside. 141 pp.

Hills, J.W. (1934). *River keeper, the life of William James Lunn*. Geoffrey Bles Ltd., London. 227 pp.

Humpesch, U.H. (1980). Effect of temperature on the hatching time of eggs of five *Ecdyonurus* spp. (Ephemeroptera) from Austrian streams and English streams, rivers & lakes. *Journal of Animal Ecology* **49**, 317-333.

Humpesch, U.H. & Elliott J.E. (1980). Effect of temperature on the hatching time of eggs of three *Rhithrogena spp.* (Ephemeroptera) from Austrian streams and an English stream and river. *Journal of Animal Ecology* **49**, 643-661.

Tokeshi, M. (1985). Life-cycle and production of the burrowing mayfly, *Ephemera danica*: a new method of estimating degree-days for growth. *Journal of Animal Ecology* **54**, 919-930.

Wright, J.F., Hiley, P.D. & Berrie, A.D. (1981). A nine-year study of the life cycle of *Ephemera danica* Müller. (Ephemeridae: Ephemeroptera) in the river Lambourn, England. *Ecological Entomology* **6**, 321-331.